Were mammals originally venomous?

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The extratarsal spur in extant monotremes consists of an os calcaris and a cornu calcaris. A poisonous extratarsal spur occurs only in the platypus (*Ornithorhynchus*); a possibly secondarily non-poisonous spur is present in echidnas (*Tachyglossus* and *Zaglossus*). Some therian mammals (e.g., bats), reptiles (*Chamaeleo*), and amphibians have a spur-like structure in the ankle, but this is not homologous to the extratarsal spur of monotremes. Among fossil mammals, the co-ossified os calcaris and ossified cornu calcaris have been found in the eutriconodontan *Gobiconodon* and in the spalacotheroid "symmetrodontan" *Zhangheotherium*. Here we describe the os calcaris in several multituberculate mammals from the Late Cretaceous of the Gobi Desert, Mongolia. The multituberculate os calcaris is a large, flat bone, generally similar to that in males of the extant monotreme species, but the cornu calcaris is not ossified. In *Gobiconodon* and *Zhangheotherium* the ossified cornu calcaris is fused to the os calcaris probably to provide the bony support for the keratinous spur. We hypothesize that the os calcaris in these Mesozoic mammal groups is homologous to that of monotremes. However, the extratarsal spur has not been found in non-mammalian cynodonts nor in other synapsids. A platypus-like os calcaris might be an apomorphic characteristic of basal Mesozoic mammals and is secondarily lost in crown therians; the os calcaris is confirmed to be absent in well-preserved tarsal structures of the earliest known crown therian mammals. We speculate that the os calcaris, the cornu calcaris, and its associated venom gland might have served the function of a defensive structure during the "dark ages" of mammalian history, when dinosaurs ruled the Earth. This structure is a plesiomorphic character retained in extant monotremes and cannot be used as an autapomorphy of Monotremata.

Key words: Multituberculata, Monotremata, *Gobiconodon*, *Zhangheotherium*, os calcaris, cornu calcaris, extratarsal spur.

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Introduction

Various tetrapods have developed a venom delivery system for killing prey and for defense. Most venomous structures are associated with the mouth (Bücherl et al. 1968; Fox and Scott 2005), but a poisonous spur can also be developed on the hind legs. The best known example in extant mammals is the extratarsal spur in monotremes, in which a venom delivery structure is supported by the cornu calcaris and is associated with the os calcaris of the tarsus. Several other tetrapods have bony projections from the tarsus that superficially resemble the os calcaris of monotremes, but they are not part of a venom apparatus. For example a spur-like prehallux is seen in some placentals and marsupials, in articulation with naviculare (Emery 1901; Lewis 1964, 1989); many microchiropteran bats are known to have a calcar bone, a slender cartilaginous or bony spur that projects from the calcaneus for supporting the interfemoral part of the wing membrane (Schutt and Simmons 1998); in reptiles, males of *Chamaeleo calyptratus* have a tarsal spur at hatching (Schmidt 1999); and in amphibians the toad *Rhinophrynus dorsalis* has a large tarsal spur (Mivart 1874).

Since the discovery of the platypus—*Ornithorhynchus anatinus* (Shaw, 1799), in the late eighteenth century (Moyal 2001), its venom-conducting spur has caught the attention of many naturalists. Even Charles Darwin in *The Descent of Man* (1881: 502) commented on it: "[...] the adult male ornithorhynchus is provided with a remarkable apparatus, namely a spur on the foreleg, closely resembling the poison-fang of a venomous snake; but according to Harting, the secretion from the gland is not poisonous; and on the leg of the female there is a hollow, apparently for the reception of the spur." Of course, the spur is in fact on the hind limb in all male monotremes and is part of a venom delivery system in the platypus (*Ornithorhynchus*), but not in the echidna (*Tachyglossus*), see Grassé (1955) and Griffiths (1968, 1978).

Jenkins and Schaff (1988) were the first to describe an extratarsal spur in a Mesozoic mammal. They referred an isolated extratarsal spur to the eutriconodontan *Gobiconodon ostromi* from the Early Cretaceous Cloverly Formation of Montana (MCZ 19860). The next extratarsal spur of a fossil mammal was discovered by Hu et al. (1997) in the spalacotheroid "symmetrodontan" *Zhangheotherium* from the Lower Cretaceous Yixian Formation of Liaoning Province, China

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(IVPP V7466). Hu et al. (1997: 140, fig. 1) designated the small L-shaped bone, preserved at the distal end of the fibula on the left side of the specimen, as "an external pedal spur".

In this paper, we will re-examine the anatomical characteristics of the extratarsal spur in extant monotremes, describe the extratarsal spur, or its component, the os calcaris in multituberculates, and then examine the comparative morphology of this structure in Mesozoic mammals.

We follow the transcription of Mongolian names proposed by Benton (2000).

Institutional abbreviations.—AMNH, American Museum of Natural History, New York, USA; CAGS, Chinese Academy of Geological Sciences (Institute of Geology), Nanking, China; CMNH, Carnegie Museum, Pittsburgh, USA; NGMC-GMV, National Geological Museum of China, Beijing; China; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Academia Sinica, Beijing, China; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass., USA; PM, Paleontological Center of the Mongolian Academy of Sciences, Ulaanbaatar, Mongolia; ZMO, Zoological Museum, University of Oslo, Norway; ZPAL, Institute of Paleobiology, Polish Academy of Sciences, Warsaw, Poland.

Structure of the extratarsal spur in monotremes

In the tarsus of monotremes, there occur two supernumerary bones, the os calcaris and os tibiale; Meckel (1826), in his monograph on *Ornithorhynchus*, confused them. The confusion lasted for almost a century (e.g., Manners-Smith 1894) and Leche (1900) even homologized the two bones. When Emery (1901) studied the hand and foot of *Tachyglossus aculeatus* (then referred to as *Echidna hystrix*) and its embryological development, he demonstrated that the os calcaris ("Spornknochen" in his terminology) is developed later in embryogenesis than the os tibiale "[…] der Spornknochen ein Hautknochen ist und aus Bindegewebe verknöchert" (Emery 1901: 673), and that the os tibiale is developed together with the other tarsal bones. Lewis (1963) followed Emery and recognized the two bones as separate units. The main argument of Lewis was the attachment of the musculus tibialis posterior to the os tibiale; the muscle continues beyond the astragalus in *Tachyglossus* and *Ornithorhynchus*. Lewis (1964: 198) described the os calcaris in *Ornithorhynchus* as a "[...] flat bony mass formed about the base of the horny perforated spur which conveys to the exterior the secretion of the femoral (poison) gland." The os calcaris is attached to the astragalus by a ligament and articulates through a small synovial joint with the tibia. Between these attachments, the os calcaris bridges over the tendons of two muscles, the tibialis posterior and the flexor tibialis, as they enter the foot. The tendon of the tibialis posterior has a small insertion on the os calcaris in *Ornithorhynchus*. This was also observed and well illustrated in Manners-Smith (1894: 708) and in Lewis's (1964: text-fig. 2) original drawing of the tarsus and metatarsus of *Ornithorhynchus anatinus* in plantar view, with the os calcaris bearing the horny spur lifted away from its site of articulation with the astragalus (talus) and the distal part of tibia. This drawing has been subsequently re-illustrated in several text-books and papers.

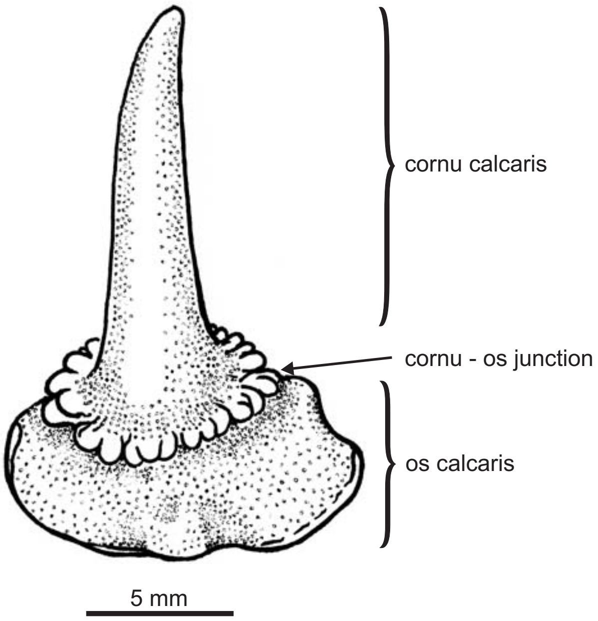

Fig 1. Basic structure of the extratarsal spur in monotremes (based on camera lucida drawing of the Recent platypus *Ornithorhynchus anatinus* (Shaw, 1799), AMNH 77856, male, left side posteromedial view. For orientation of the spur to the pes, see Fig. 3A.

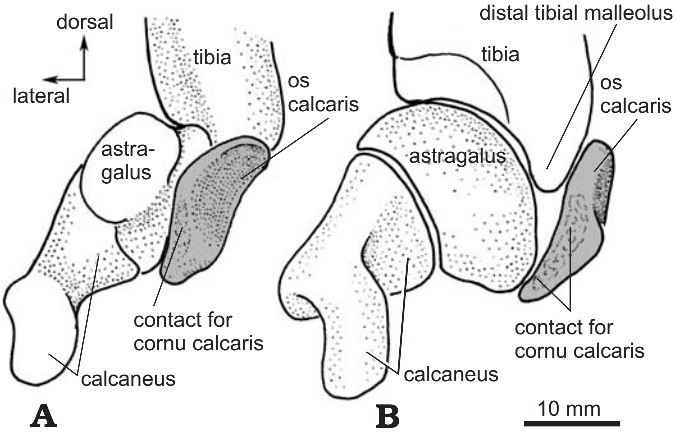

Fig. 2. Articulation of the os calcaris to the surrounding bones in the Recent *Ornithorhynchus anatinus* (Shaw, 1799), AMNH 65833; male, left ankle joint. **A**. Posterolateral view. **B**. Posterior view. The cornu calcaris has been removed and the partially disarticulated ankle joint has exposed the contact relationship of the os calcaris to the distal tibial malleolus and to the astragalus.

In this paper, we accept the terminology of Lewis (1963, 1964) with some additions. The os calcaris is connected to the cornu calcaris or the core of the spur itself and has a bone-to-bone contact to the astragalus and the distal end of the tibia near the junction of the two bones (see discussion below on how to distinguish the os tibiale from os calcaris in fossils).

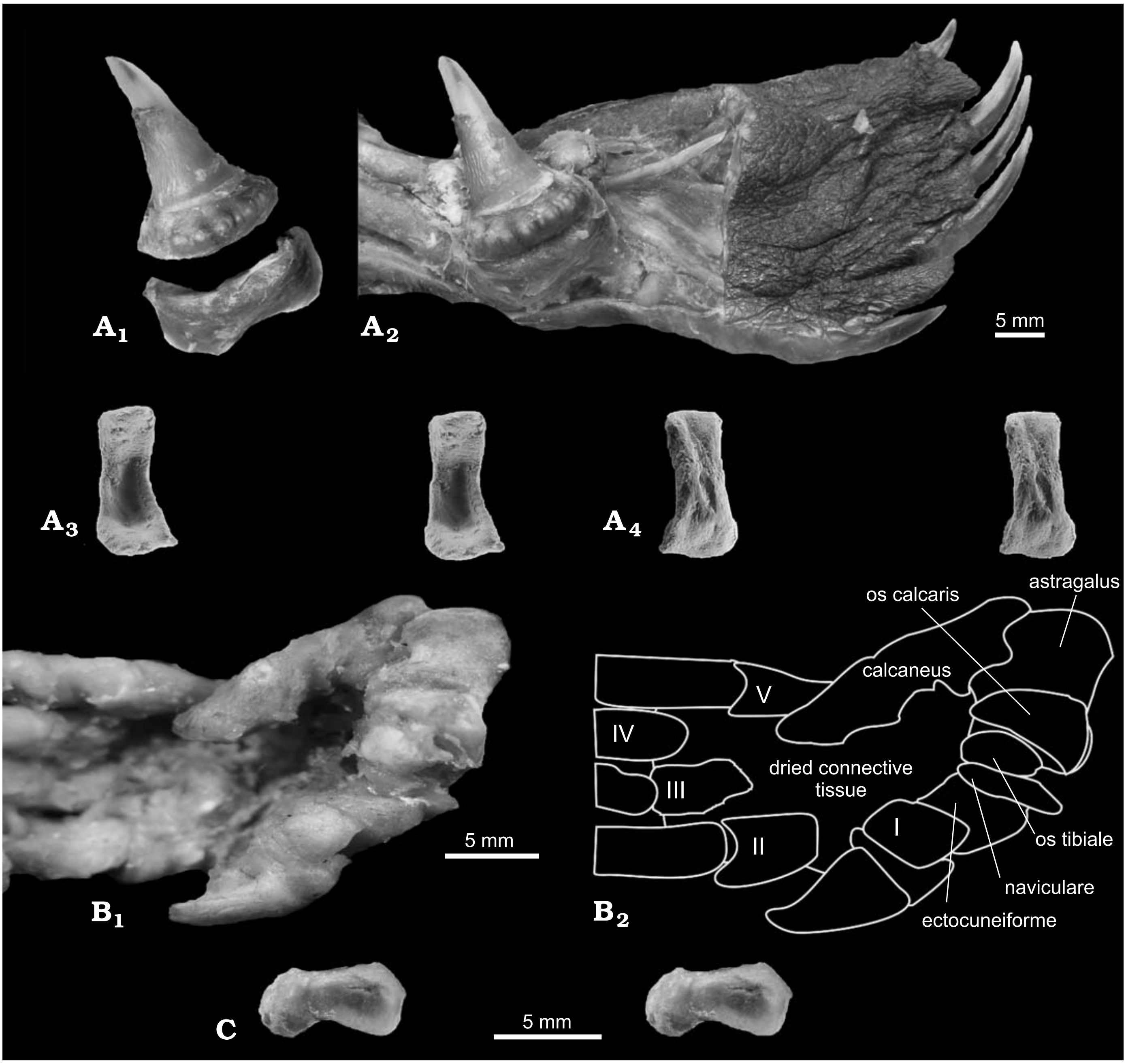

Fig. 3. Os calcaris in the Recent monotremes. **A**. Partial left tarsus of *Ornithorhynchus anatinus* (Shaw, 1799), ZMO 11793, an adult male. Cornu calcaris and its keratinous sheath and os calcaris removed from the tarsus (A_1); tarsus partly dissected (A_2); isolated os calcaris of the same specimen, stereo-photo of the medial side showing the concave inner side (A_3); isolated os calcaris of the same specimen, stereo-photo of the lateral side showing rough surface (A_4). **B**. Left tarsus of *Tachyglossus aculeatus* (Shaw, 1792), ZPAL Mw-3 in plantar view with os calcaris preserved (B_1), and explanatory drawing of the same (B_2). Roman numerals I–V denote the fingers. **C**. Stereo-photo of lateral side of disarticulated os calcaris from the right tarsus of the same individual.

The second confusion in terminology is the use of the multiple names: spur, tarsal spur, extratarsal spur, external pedal spur, and os calcaris for the same bony structure. We use the term os calcaris for the plate-like bony base in articulation with the astragalus or calcaneus, and sometimes the distal end of the tibia (here some intraspecific variation is observed in monotremes); while the term cornu calcaris (*sensu* Gregory 1947: 36; horny spur of Calaby 1968: 21) is used for the keratinous spur; and the bony core structure inside the keratinous spur is termed ossified cornu calcaris. Finally, we use the term extratarsal spur for the entire structure made up of the os calcaris (the base), the ossified cornu calcaris (the core), plus cornu calcaris, the keratinous spur (Fig. 1). The distinction between these structures of the extratarsal spur of modern monotremes will have important implications for the comparative studies of the similar structures in Mesozoic mammals, as one component, the base of the extratarsal spur tends to be more often preserved than the other two.

In fossil mammals, the most frequently preserved structure is the os calcaris, or the plate-like bony base of the extratarsal spur. The ossified cornu calcaris is co-ossified with the os calcaris in some Mesozoic mammals (see below). The keratinous sheath of the spur is usually not preserved but may be seen as a part of an impression in *Aikidolestes* (Li and Luo 2006), a rare case of soft-tissue preservation in the Yixian Formation of China. We also point out that the extratarsal spur is a sexually dimorphic feature in modern monotremes; the keratinous spur is absent in adult female platypus (Calaby 1968; Griffiths 1968, 1978) and vestigial or absent in adult female echidnas. Griffiths (1978: 25) stated: "As in *Ornithorhynchus*, the inside of the ankle [of *Tachyglossus*] in all males bears a hollow perforated spur only 0.5–1.0 cm long; juvenile females also can exhibit a small sharp spur which is lost later in life; thus if an echidna lacks a spur on the ankle it is certainly a female." With respect to *Zaglossus* Griffiths (1978: 75) wrote: "Of eight *Zaglossus* specimens I have examined and whose sex was determined by dissection, six were males and had spurs on the ankle. Of the females 7.4 kg and 4.5 kg in weight respectively, the smaller one, which had never bred [...] had spurs; this animal when first examined was deemed to be a male but dissection proved it to be a female. The other female, the larger one, had bred and she had not spurs. This suggests that juvenile female *Zaglossus* have spurs just as some juvenile *Tachyglossus* females do."

It follows that the distribution of this feature may be under represented in fossil taxa due to its sexually dimorphic nature.

The os calcaris is known to occur in adult males of all three species of living monotremes. The keratinous spur occurs in young females of platypuses and then disappears in adults, and the bony os calcaris possibly disappears as well. During the work on this paper, we studied the tarsi of more than a dozen specimens of *Ornithorhynchus anatinus* and *Tachyglossus aculeatus* belonging to both sexes at various ontogenetic stages, and we illustrate some of them.

The os calcaris of *Ornithorhynchus* (Figs. 2 and 3A) is a flat, and plate-like bone. It is situated below and lateral to the horny spur. It is attached to the posterior aspect of the astragalus and the distal tibial malleolus by a ligament. The side facing the astragalus (the inner side) tends to be slightly concave and corrugated. The external surface tends to be undulating and has a deep central groove in some specimens (Fig. 3) or a slightly concave surface in others (Fig. 2). Its proximo-lateral margin is slightly convex, and its disto-medial margin tends to be slightly concave. The overall outline of this plate-like bone is variable with size. Smaller ossa calcares are bean-shaped. Slightly larger ossa calcares may have a more convex lateral border. The largest os calcaris examined by us (AMNH 77856) is oblong in outline with a triangular margin (Figs. 1 and 2), but others are rectangular. The lateral (or proximo-lateral) margin is thickened, bulging and rugose (Fig. 2), for the attachment of the cornu calcaris. The cornu calcaris is attached to the os calcaris by a zone of cartilage, and the periphery of this junction is moderately or heavily crenulated (Figs. 1 and 3A). The conical core of the spur is slightly curved and bent distal to its junction with the os calcaris, so it points posteriorly. The length of the cornu is intraspecifically variable. The cartilage junction between the os calcaris and the cornu calcaris could absorb some of the impact when the spur is forced into flesh.

In *Tachyglossus*, the os calcaris is situated on the plantar side of the tarsus (Fig. 3B). It is a small bone of roughly rectangular shape attached to the astragalus. The bone is placed close to the os tibiale and may easily be confused with that bone. The os tibiale is much smaller and more rounded than the os calcaris and is situated partly between the astragalus and naviculare (see e.g., Lewis 1963: fig. 2b; Gambaryan et al. 2002: fig 5c). As in *Ornithorhynhus*, the os calcaris is attached to the astragalus medially by a fibrous union. The medial surface is concave and smooth. In *Ornithorhynchus*, the os calcaris provides a relatively extensive support for the cornu calcaris, but in *Tachyglossus* the supporting function of os calcaris for the cornu calcaris is nearly lost, the bone being tightly connected to the astragalus. Fig. 3B shows the position of the os tibiale and os calcaris in the left tarsus of *Tachyglossus*. Fig. 3C shows the disarticulated right os calcaris from the same individual. The bone is oriented with its lower margin being the surface close to the os tibiale in the articulated specimen.

In summary, the size and outline of the os calcaris is variable in monotremes. The conical morphology of the cornu calcaris is more conserved but its length and curvature are variable. The attachment of the os calcaris to other tarsal bones is different between the echidnas and the platypus. From the practical purpose of recognizing the extratarsal elements (separate or fused os calcaris and ossified cornu calcaris) in fossils, we also note that in some taxa, the os calcaris and ossified cornu calcaris tend to be fused, such that the entire extratarsal elements would be preserved as one fossilized extratarsal structure (see below). The os tibiale in living monotremes is a sesamoid bone associated with m. tibialis posterior. If present at all, the os tibiale tends to be smaller and more rounded, with a more anterior and more plantar position, than the os calcaris. Hence, if these two supernumerary bones in the tarsus are preserved in fossils, it is possible to distinguish them.

Os calcaris in multituberculates

In all three multituberculates described below, we found only the os calcaris part of the extratarsal spur. If an ossified cornu calcaris was present it was not co-ossified with the os calcaris.

***Catopsbaatar catopsaloides* (Kielan-Jaworowska, 1974)** (Fig. 4A).—The os calcaris is preserved *in situ* on the left pes of PM 120/107 from the Hermiin Tsav locality, the Upper Cretaceous red beds of Khermiin Tsav (stratigraphic equivalent of the Baruungoyot Formation), Gobi Desert, Mongolia. This skeleton of *Catopsbaatar* received a preliminary description (Kielan-Jaworowska et al. 2002), while its skull has been described in detail by Kielan-Jaworowska et al. (2005).

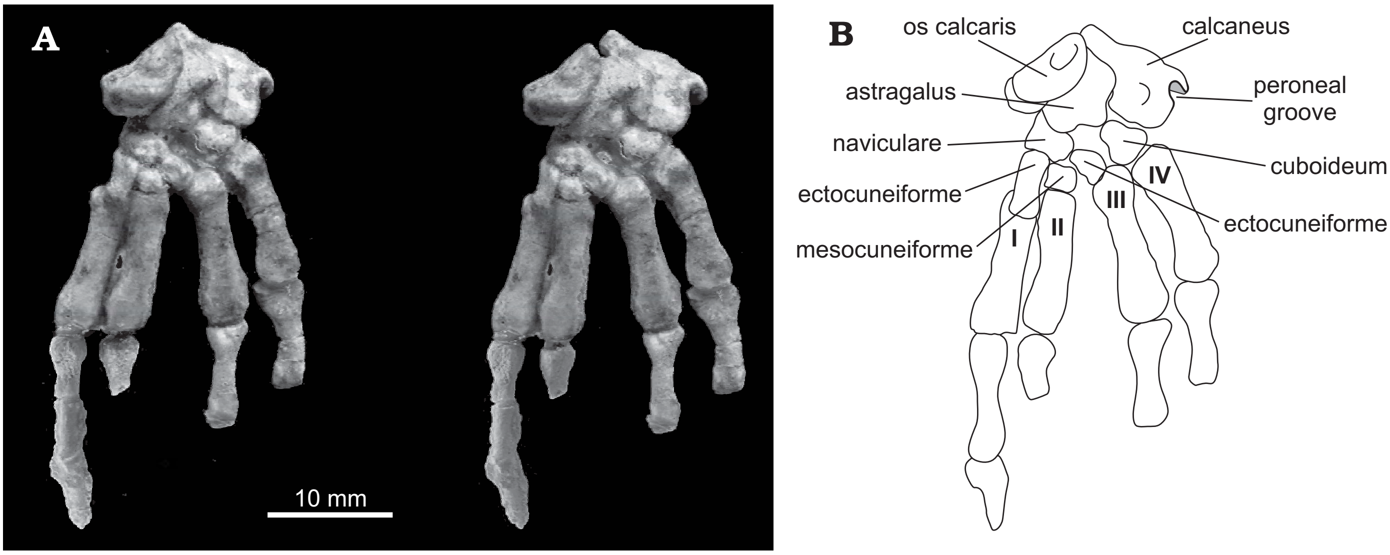

Fig. 4. Os calcaris in multituberculates. Left tarsus of *Catopsbaatar catopsaloides*, PM 120/107. **A**. Stereo-photo in dorsal view. **B**. Explanatory drawing of the same. The V finger, preserved separately, has not been reconstructed. Upper Cretaceous, red beds of Hermiin Tsav (equivalent of the ?upper Campanian Baruungoyot Formation), Hermiin Tsav II, Gobi Desert, Mongolia.

We provide here information on the os calcaris of this specimen. Fig. 4A shows the tarsus in dorsal and plantar view. Several tarsals of this multituberculate are slightly displaced. The metatarsals are all present in the specimen, but metatarsal V is displaced and was found next to the knee joint of the left leg. The displaced metatarsal V is identified by its articulation surfaces for the cuboid and for calcaneus. The os calcaris might be correctly situated on the medial side of astragalus but there is a possibility that it has slightly moved from the plantar side of the metatarsus to the medial side. The bone itself is plate-like and its outline is rectangular in medial view. The medial surface is smooth except for a small tubercle. The placement of the os calcaris in the ankle of *Catopsbaatar* is more medial than in *Ornithorhynchus*, but the extratarsal spur (cornu calcaris not preserved in fossil) would point medially in both taxa by comparison of the structural

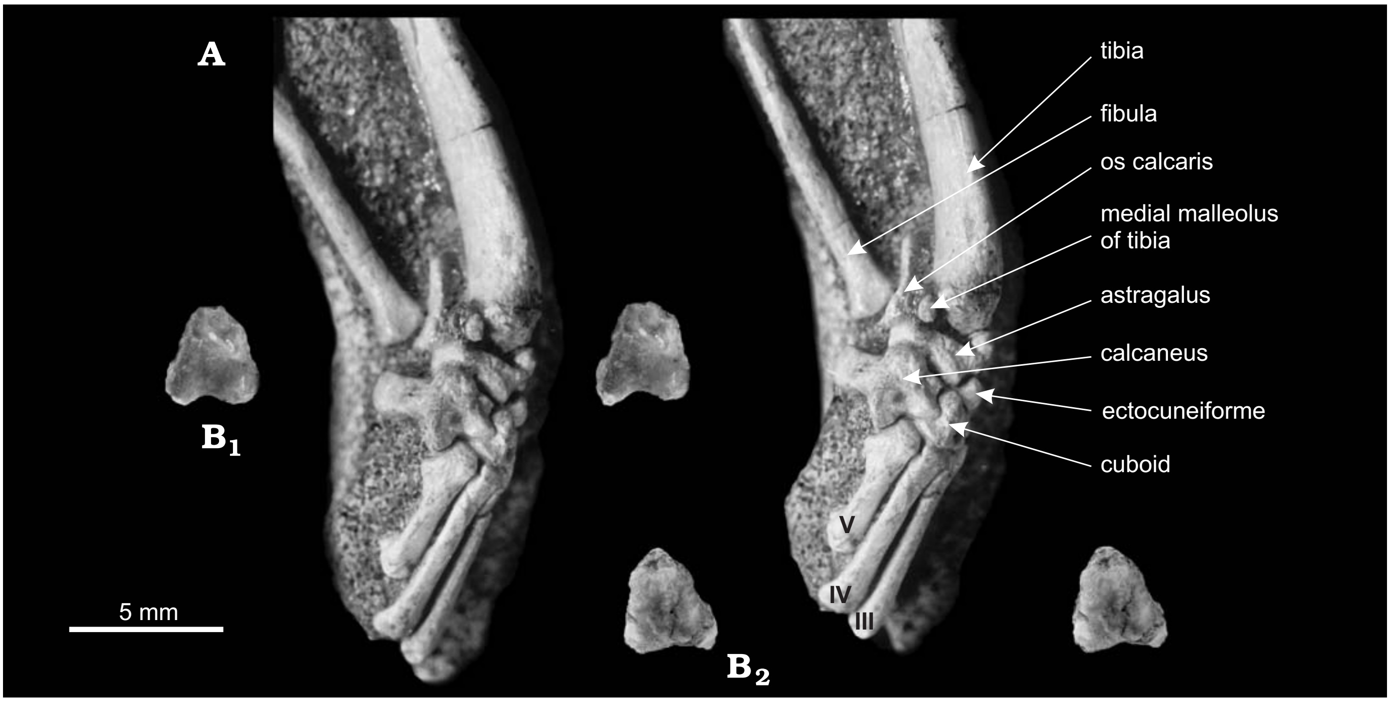

Fig. 5. Os calcaris in multituberculates. **A**. Stereo-photograph of the right tarsus of *Kryptobaatar dashzevegi*, ZPAL MgM-I/41, in lateral view, showing partly exposed os calcaris, situated between the distal ends of the tibia and fibula. **B**. Stereo-photos of the left os calcaris (incomplete) of the same animal, in ?ventral (B_1) and ?dorsal (B_2) views. Upper Cretaceous Djadokhta Formation (?lower Campanian), Bayan Zak, Gobi Desert, Mongolia.

relationship between the os calcaris and cornu calcaris in *Ornithorhynchus*.

Kryptobaatar dashzevegi **Kielan-Jaworowska, 1970** (Fig. 5).—The os calcaris is preserved in the ankle joint of ZPAL MgM-I/41, from the Upper Cretaceous Djadokhta Formation, of Bayan Zag, Gobi Desert, Mongolia. Kielan-Jaworowska and Gambaryan (1994: fig. 2) published a photograph of the ankle joint of this specimen but did not describe the os calcaris. Wible and Rougier (2000: 7) noted that the "tarsal spur" was present in this multituberculate. Here we provide additional description and photographic documentation of the os calcaris.

We interpret that the os calcaris was present in *Kryptobaatar*, but the ossified cornu calcaris was not co-ossified or not present and therefore missing from ZPAL MgM-I/41. In this skeleton (Fig. 5A), the os calcaris is preserved in its entirety on the right side of the specimen between the distal ends of the tibia, fibula, and astragalus.

The right os calcaris of the same specimen has been preserved between the distal part of the fibula and the astragalus (Fig. 5; also see fig. 2a of Kielan-Jaworowska and Gambaryan 1994). It was impossible to prepare this bone from the surrounding matrix and bones without causing damage to other bones. Nonetheless, half of this bone is exposed and appears to be relatively complete; and it is plate-like with either an oblong or rectangular outline, with a pointed apex and a ventral process extending horizontally below the fibula, but it resembles very closely the complete os calcaris of *Catopsbaatar* (Fig. 4).

The left os calcaris of ZPAL MgM-I/41 has been displaced from the vicinity of the tarsus and is preserved close to the base of the epipubic bone (Kielan-Jaworowska and Gambaryan 1994: fig. 2B). It was possible to remove the bone from the matrix. We interpret that the left os calcaris is not complete (Fig. 5B). As preserved, it is approximately half the size of the complete os calcaris on the right side. The preserved portion is plate-like, and has a roughly triangular outline, with rounded lower corners and slightly concave lower margin. In the right lower corner, there is an oblique wide furrow extending from the margin anteromedially (Fig. 5B).

Chulsanbaatar vulgaris **Kielan-Jaworowska, 1974**.—An os calcaris, broken into two pieces, is preserved in ZPAL MgM-I/99b (not illustrated here). The partial left tarsus of *Chulsanbaatar vulgaris* was described and illustrated by Kielan-Jaworowska and Gambaryan (1994: fig. 25). We now interpret that a partial os calcaris is preserved *in situ*, and maintains its articulation with the astragalus/calcaneus. This structure was previously labeled as "?tibia" in Kielan-Jaworowska and Gambaryan (1994: fig. 25). Another part of this os calcaris is preserved in association with the distal end of the left fibula (Kielan-Jaworowska and Gambaryan 1994: fig. 17A). The bone can be seen in medial and plantar views but it is very fragmented and partially covered with glue and sediments; hence, the rest of its outline is difficult to reconstruct from the two preserved fragments.

Not all multituberculates with well-preserved ankles have shown an extratarsal structure. For example, this structure is absent in the ankle of the only known postcranial specimen of *Sinobaatar* (Hu and Wang 2002). We were able to confirm the original observation that the extratarsal spur is also absent in the specimens so far known of the Tertiary multituberculate *Ptilodus* (Krause and Jenkins 1983).

Extratarsal spur in eutriconodontans

Gobiconodon ostromi **Jenkins and Schaff, 1988** (Fig. 6).—Jenkins and Schaff (1988: 18) described the extratarsal spur (referred to as a "spur-like element") of the eutriconodontan *Gobiconodon ostromi* as follows: "The base is an oval nodule, rounded on the external surface that bears the spur; the internal surface is flat, except along the edge adjacent to the spur, which is raised in the form of a small process. The spur is set eccentrically on the external surface, is constricted about its base, and tapers toward the apex, which is broken off." (See also Jenkins and Schaff 1988: fig. 18).

We supplement their description with more detail photographs of a cast of the extratarsal spur (Fig. 6). We interpret the oval base or plate to be the equivalent of os calcaris. The "spur" itself is the ossified cornu calcaris, and the slight con-

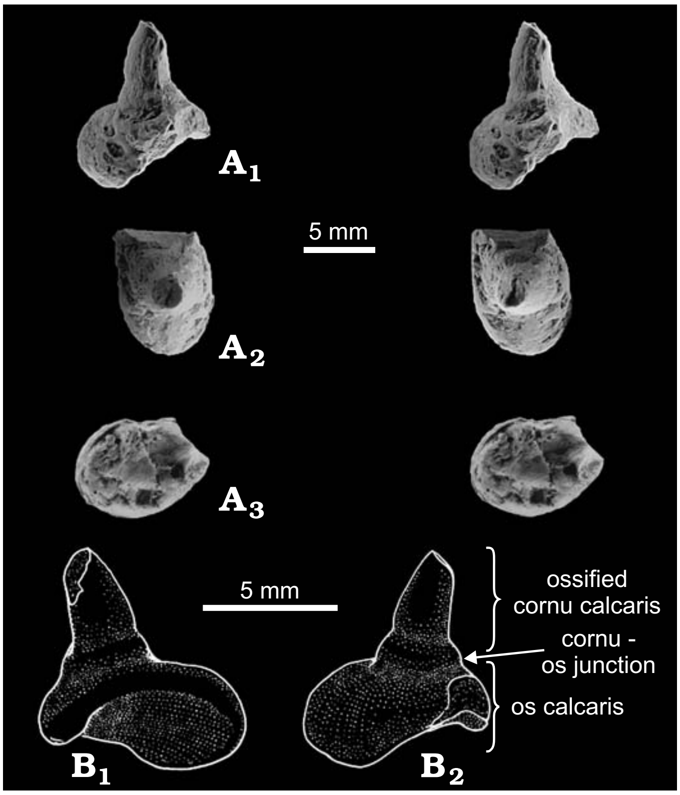

Fig. 6. Extratarsal spur in the eutriconodontan *Gobiconodon*. **A**. Stereo-photos of a cast of os calcaris of *Gobiconodon ostromi*, MCZ 19860 (see also Jenkins and Schaff 1988). Lateral extratarsal spur in dorsal view (A_1). The same from the apical view of the ossified cornu calcaris (A_2). The "under" or "inner" surface of the os calcaris of the same (A_3). **B**. Illustration from camera lucida drawing of the extratarsal spur in ventral (B_1) and dorsal view (B_2). Lower Cretaceous, Cloverly Formation, Montana.

striction between the cornu calcaris and the ossified os calcaris represents the fused junction of these two structures (Fig. 6). Therefore, the "spur-like element" as recognized by Jenkins and Schaff represents the entire extratarsal spur, minus the keratinous sheath on the outer surface of the cornu.

The ankle joints of the eutriconodontan *Jeholodens jenkinsi* (Ji et al. 1999) are well preserved in specimen NGMC-GMV 2139a; but the extratarsal spur or its components are not present in this fossil. We speculate that the absence of this feature is due to the sexually dimorphic nature of this character. Specimens of the gobiconodontid *Repenomamus* have been found by the dozens (J.-L. Li et al. 2001; C.-K. Li et al. 2003; Hu et al. 2005), but not described in detail. It might be possible to test the frequency of this dimorphic structure among the individuals of these species, or possibly use this feature to determine the sexes of the relatively well preserved skeletal fossils of this group.

Extratarsal spur in "symmetrodontans"

Zhangheotherium quinquecuspidens **Hu, Wang, Luo, and Liu, 1997** (Fig. 7).—Hu et al. (1997) reported the presence of "an external pedal spur"' in IVPP V7466 from the Early Cretaceous of Liaoning Province, China. The bone is shown schematically as an L-shaped structure in their fig. 1, which depicts the entire skeleton of the holotype. The "external pedal spur" of *Zhangheotherium*, as illustrated by Hu et al. (1997), is the equivalent to the bony extratarsal spur structure. The oblong base, os calcaris, and the large ossified cornu calcaris are the two arms of the "L-shaped" extratarsal spur (Fig. 7). The smaller and more pointed arm of the "L-shaped" structure is the ossified cornu calcaris. This structure is similar to that of *Gobiconodon* in the co-ossification of the cornu and os calcaris. However, it should be noted that the extratarsal spur is not present in the ankle of a second *Zhangheotherium* specimen (CAGS-IG99-07352; Luo and Ji 2005). The tarsals of this specimen are scattered as preserved. It is not clear if the absence of extratarsal spur (or os calcaris) is due to poor preservation, or that this specimen is a female.

Rougier et al. (2003) reported on a second zhangheotheriid species, *Maotherium sinensis* (NGMC-97-4-15). Although the extratarsal spur was not described, this structure is preserved in both ankle joints in the holotype of *Maotherium*, as shown in the photographs (Rougier et al. 2003: plate II-D). The *in situ* preservation and the orientation of the ossified cornu calcaris are almost identical to the preserved extratarsal bony spur of IVPP V7466 (*Zhangheotherium*). *Z. quinquecuspidens* and *Maotherium sinensis* demonstrate that the bony part of the extratarsal spur (os calcaris and ossified cornu calcaris) is a basic feature in acute-angled "symmetrodotontans" and is a plesiomorphic feature in technotherians (*sensu* McKenna and Bell 1997; Luo et al. 2002; Kielan-Jaworowska et al. 2004).

Discussion and conclusion

Are the extratarsal spur structures seen in the different Mesozoic mammals homologous with those of extant monotremes? The answer is clearly yes. However, the most frequently preserved component of the extratarsal spur structure in fossil state, is its base of support, the os calcaris; the ossified cornu calcaris and its keratinous sheath are often not preserved as in the case of multituberculate specimens we have examined. But from the anatomical association of the os calcaris and cornu calcaris in living monotremes, we infer that the entire extratarsal spur structure possibly was present in multituberculates.

In *Gobiconodon*, the extratarsal spur can be recognized and it consists of the base (os calcaris) and a bony inner support for a spur (ossified cornu calcaris), but the horny sheath of the extratarsal spur is not present. The extratarsal spur in *Zhangheotherium* closely resembles that in *Gobiconodon*. The flat rectangular bones found in multituberculates have only tiny ridges on the surface, suggesting that they are reduced compared to those of *Zhangheotherium* and *Gobiconodon*. The bones lack the bony inner support for a spur

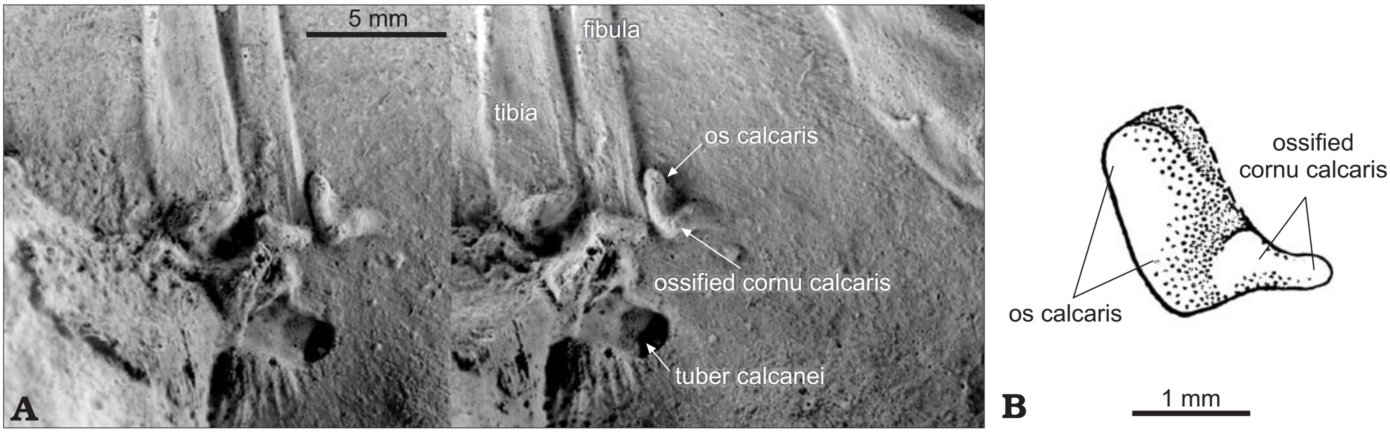

Fig. 7. Extratarsal spur of *Zhangheotherium quinquecuspidens*. **A**. Stereo-photo of a silicone cast of the tarsus and extratarsal spur of *Zhangheotherium*, IVPP V7466 (see also Hu et al. 1997). **B**. Interpretive drawing of the structure of extratarsal spur (reconstruction from IVPP V7466 and a CAGS specimen from Luo and Ji, 2005). Lower Cretaceous, Yixian Formation, Liaoning Province, China.

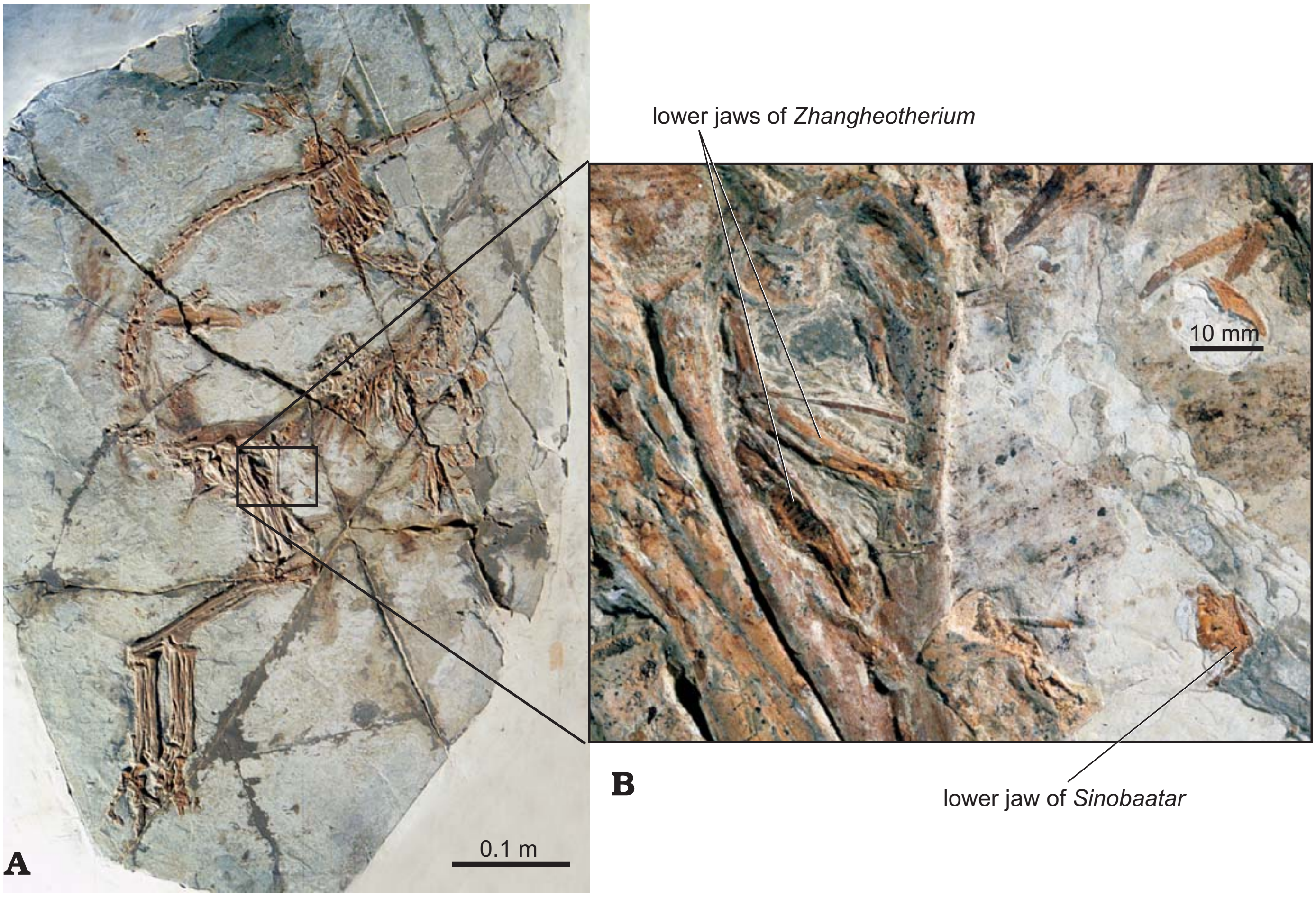

Fig. 8. Two mammals (represented by three specimens) in a stomach of a small carnivorous dinosaur. **A**. *Sinosauropteryx prima* (GMV 2124), entire specimen. **B**. Enlarged abdominal contents in the pelvic area of the same. Lower Cretaceous, Yixian Formation, Liaoning Province, China.

and appear to have served only as a base for a keratinous sheat. The placement of the os calcaris in *Catopsbataar* is more medial than in *Ornithorhynchus*, but the spur would have pointed medially as in the monotremes.

In *Gobiconodon* and *Zhangheotherium* the spur is not only supported at its base by the os calcaris, as is seen in monotremes and inferred in multituberculates, but a bony spur is present. In monotremes the spurs are hollow and therefore may be used to inject poison. The bony spur of *Gobiconodon* has probably been sheathed by a keratinous spur, but a groove for a poison canal is not seen in the bony spur. This may have limited the function of the spur, suggesting that it may have been non-venomous. The same may be inferred from the small L-shaped bone in *Zhangheotherium*. It is difficult at present to venture an opinion whether this is a secondary loss of a venom delivery system, as seen in *Tachyglossus*, or whether the ancestral condition would be non-venomous.

Beginning with their appearance in the Carnian (about 225 MA ago) until the end of the Cretaceous (65.5 MA ago), mammals were almost exclusively small creatures of probable nocturnal habits (Jerison 1973; Kielan-Jaworowska et al. 2004). With exception of Early Cretaceous *Repenomamus*, few Mesozoic mammals attained the size of a fox. Most Mesozoic mammals were probably too small to serve as prey for large theropod dinosaurs; but some small-size dinosaurs (troodontids, dromaeosaurids, and oviraptorosaurians), large lizards, crocodiles, birds, and even large sphenodontians could well have preyed on them. Some of the large mammals, such as the large individuals of the stem mammal *Sinoconodon* in the Early Jurassic (Crompton and Sun 1985; Crompton and Luo 1993), the gobiconodontid *Repenomamus* of the Early Cretaceous (J.-L. Li et al. 2001; Hu et al. 2005), and the marsupial *Didelphodon* of the Late Cretaceous (Clemens 1966) could also have preyed on smaller mammals.

One of us (JHH) found that in the abdomen of a specimen (CAGS GMV 2124) of the feathered dinosaur *Sinosauropteryx prima*, three lower jaws of mammals have been preserved (Fig. 8), rather than two as previously mentioned by Ackerman (1998). Two of them belong to *Zhangheotherium*, the third to the multituberculate *Sinobaatar* (Hu and Wang 2002). This finding unequivocally demonstrates that small Mesozoic mammals were prey for larger carnivorous vertebrates.

For these early mammals that were small, the presence of an extratarsal spur could serve as a defensive weapon. If it was also part of a venom delivery system it would have been doubly effective. In the venom delivery system of the platypus, the spur is connected to the venom-secreting femoral gland. The spurs are situated on the inner side of the tarsus, and the left and right spurs are directed towards one another. Calaby (1968: 26) described the use by platypuses of their poisonous spur on man, as follows: "When attacking, the platypus drives the hind legs toward one another with considerable force so that the spurs are embedded in the flesh caught between [in case of man, usually the hand or wrist]. In at least some cases difficulty was experienced in forcing the legs of the animal apart so that the victim could be released." Undoubtedly, the extratarsal structure is useful for defending against natural enemies. It has also been documented that the apparatus was employed to attack other male platypuses and possibly for hunting.

To date, the bony extratarsal spur or its os calcaris have been described only in three groups of Mesozoic mammals: eutriconodontans, "symmetrodontans" and multituberculates. This structure is most likely a characteristic of the entire monotreme group (Fig. 9). The presence of an extratarsal spur is not a synapomorphy of crown mammals as indicated by distribution of this feature in the phylogeny of major Mesozoic mammal groups (Luo et al. 2002; Kielan-Jaworowska et al. 2004). Although tarsals are not preserved in the Late Jurassic docodontan *Haldanodon* (Krsuat 1991; Martin 2005), the os calcaris is now known from a new docodontan from China (Luo, personal observation 2005). Presence of the extratarsal spur in morganucodontans (Jenkins and Parrington 1976) has not been demonstrated as yet since the tarsals are incompletely known in this group.

Modern marsupials and placentals clearly have lost the extratarsal spur. So far, this feature has not been reported in any Cretaceous eutherians (Kielan-Jaworowska 1977, 1978; Novacek et al. 1997; Horovitz 2000; Ji et al. 2002). It is also true that this structure is absent from the relatively complete ankles as known for early marsupials and stem metatherians (Muizon 1995; 1998; Szalay and Trofimov 1996; Luo et al 2003). It follows that the extratarsal spur (and possibly its associated venom gland) is absent from therian mammals.

The condition of the extratarsal spur is unknown in major Mesozoic mammalian groups more derived than spalacotherioids but more primitive than crown therians. The ankle joint as known for the dryolestoid *Henkelotherium* is not complete (Krebs 1991; Vázquez-Molinero et al. 2001; Vázquez-Molinero 2003). The astragalus and calcaneus of *Vincelestes* have been very well described, but it is not known if any supernumerary tarsal elements are present in this taxon (Rougier 1993).

In light of the above-discussed data, we put forward the hypothesis that the extratarsal spur is a basic feature of Mammalia and was retained in all lineages of basal Mesozoic mammals. Its main adaptive function is for defense, possibly made more effective by being associated with a venom gland. This structure is also useful to a lesser extent for intra-specific competition or predation. It is conceivable that this feature originated earlier than crown Mammalia. Within Mammalia, the extratarsal spur is secondarily lost in crown Theria, if not earlier in the precursors to crown therians (Fig. 9). The extratarsal spur in extant monotremes is a symplesiomorphic character and cannot be used to characterize the Monotremata as a monophyletic group as has been done repeatedly by some neontologists (e.g., Ax 1984; Sudhaus and Rehfeld 1992). This character shows that the reconstruction of phylogeny based only on evidence from living mammals can be misleading.

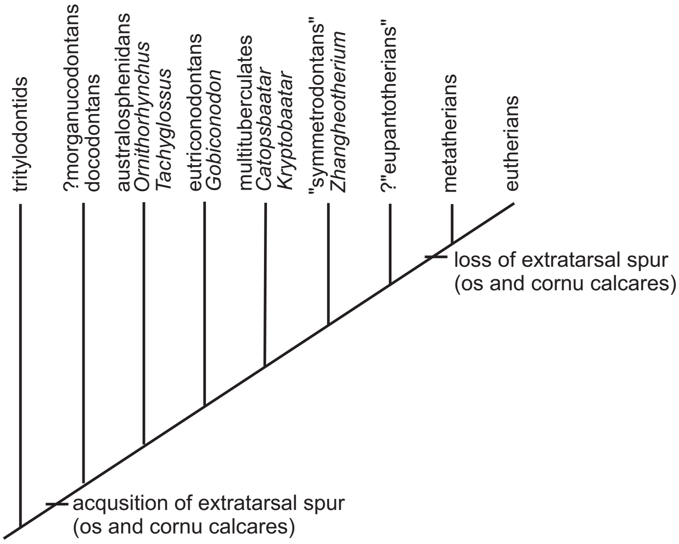

Fig 9. Tentative evolutionary pattern of extratarsal spur of the main groups of early mammals (cladogram simplified from Luo et al. 2002 and Kielan-Jaworowska et al. 2004).

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